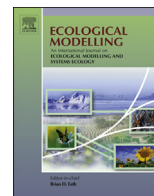




Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Modeling cougar habitat in the Northeastern United States

Henry B. Glick*

Yale School of Forestry and Environmental Studies, 195 Prospect Street, New Haven, CT 06511, USA

ARTICLE INFO

Article history:

Received 28 October 2013
Received in revised form 1 February 2014
Accepted 2 February 2014
Available online xxx

Keywords:

Puma concolor
Eastern cougar
Habitat Suitability Index
Habitat modeling
New England

ABSTRACT

While the U.S. Fish and Wildlife Service has declared the Eastern cougar (*Puma concolor couguar*) extinct, proposing to remove the subspecies from the Endangered Species List, in the Northeastern United States there are over 2300 eyewitness reports and nearly a dozen confirmed accounts of cougars. This discrepancy between what has been documented by management agencies and what has been perceived by regional residents raises questions about the current and future presence of cougars in the region, yet little work has been done to examine the Northeast's capacity to support this species. I used spatially-explicit Habitat Suitability Indices to model cougar habitat in the six New England states and that portion of New York East of the Hudson River. I present one original model and five models in which I replicated methods originally established by other authors outside of the study region. For each model I identified contiguous habitat parcels capable of supporting viable breeding populations of cougars according to two estimates of population range size. I evaluated model results by comparing the percent forested land cover within viable habitat patches to that associated with historic cougar kills. I also assessed model agreement by generating two ensemble models – one comprised of each individual model output, and one comprised of viable contiguous habitat that was coincident across all models. I found that all individual models and one ensemble model identified viable habitat according to both population range estimates, while the second ensemble model identified viable habitat according to the liberal range estimate only. Individual models identified between 20,457 and 160,971 km² of top ranking habitat, enough area to theoretically support between 322 and 2535 cougars. Collectively these models provide a set of heuristic tools that shed light on a species that could influence future trophic interactions in the region. In light of my findings and the active expansion of cougar territory into the Midwest, I recommend that regional management begin to educate local residents about the nature of human–cougar interactions, and to consider preliminary management strategies for dispersing Midwestern cougars as resources allow. I recommend also that future modeling efforts integrate human input from regional biologists, and that these models be used to help evaluate cougar sighting reliability.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Prior to colonial settlement, the geographic range of mountain lions, or cougars (*Puma concolor* L.), stretched nearly coast to coast from the Yukon province in Canada to Southern Chile (Young and Goldman, 1946; Anderson, 1983; Culver et al., 2000). Today they are common across much of Western North America, but their presence in Eastern North America is limited, as it has been for nearly a century (Dearborn, 1927; Wright, 1959; Bolgiano, 1995; McCollough, 2011). Beginning with early colonial encounters, cougars were extirpated from most of the Eastern United

States (Seton, 1929; Young and Goldman, 1946; Downing, 1982). In the Northeast specifically, the last confirmed accounts of cougars vary from as early as 1853 to 1865 in New Hampshire (Dearborn, 1927; Seton, 1929), to as recently as 1938 in Maine (Wright, 1948, see also Spargo, 1950; Stoner, 1950; Wright, 1953; Reilly, 1964).

Currently, cougars are considered extirpated in the Eastern United States by many regional biologists (T. French, Massachusetts Department of Fish and Game [MADFG], M. McCollough, Maine Department of Inland Fisheries and Wildlife [MDIFW], P. Rego, Connecticut Department of Energy and Environmental Protection [CTDEEP], C. Bernier, Vermont Department of Fish and Wildlife [VTFW], C. Brown, Rhode Island Department of Environmental Management [RIDEM], S. Van Arsdale, New York State Department of Environmental Conservation [NYSDEC], personal communication), yet eyewitness accounts of animals thought to be cougars have increased in number over the twentieth and twenty-first

* Permanent address: 100 Marble Road, Center Ossipee, NH 03814, USA. Tel.: +1 603 387 4912.

E-mail addresses: henry.glick@gmail.com, henry.glick@yale.edu

centuries (Wright, 1948; Doult, 1969; Downing, 1982; Clark et al., 2002; McCollough, 2011, and unpublished files from the CTDEEP, MADFG, MDIFW, New Hampshire Fish and Game Department [NHFGD], NYSDEC, RIDEM, and VTDFW). By 1973, when the federal Endangered Species Act (ESA) was established (U.S.C., 1973), sightings of supposed cougars were so numerous that the Eastern cougar subspecies (*P. concolor cougar*) was listed as endangered (Federal, 1973). Listing occurred even though it was unclear whether or not people were actually seeing cougars, and whether or not viable populations could exist (USFWS, 2011). Many have maintained that cougars are a lost remnant of the Eastern landscape (Young and Goldman, 1946; De Vos, 1964; Downing, 1982; McBride et al., 1993; Scott, 1998; Sunquist and Sunquist, 2002; McCollough, 2011), and a recent U.S. Fish and Wildlife Service (USFWS) five-year review (McCollough, 2011) found no evidence to support assertions that the Eastern cougar still exists. The USFWS has proposed to delist *P. concolor cougar* based on extinction.

Despite this proposal, over the last 40 years there have been as many as 10,000 eyewitness reports of cougars in the East (McCollough, 2011:38), including more than 2300 eyewitness reports and 11 confirmed accounts from the Northeast in the last 20 years alone (unpublished files from MDIFW, NHFGD, VTDFW, MADFG, CTDEEP, RIDEM, and NYSDEC; The Cougar Network, 2007, see also Bolgiano et al., 2003). Cougar sighting data is largely unreliable and impossible to verify, while confirmed accounts provide tangible evidence of cougar presence – released captives, transient males, or otherwise. The Florida panther population aside, the Northeast represents the greatest source of validated cougar evidence East of Illinois (The Cougar Network, 2007), yet little effort has been put into assessing the current landscape in light of cougar ecology. This absence has put the rigorous evaluation of potential cougar habitat high on the list of recommendations for the immediate future (Laundré and Spatz, 2011).

The critical issue in conservation of cougars in New England landscapes is whether or not there are indeed locations that provide the habitat conditions needed to support viable, breeding populations. One way to assess this potential is through the use of habitat distribution modeling. Predictive habitat models are common in ecology, and have existed in various forms for decades (Guisan and Zimmermann, 2000). Modeling relies on working hypotheses about how the physical environment, trophic dynamics, and physiological nature of a species limit its spatial distribution. Here, my focus is on spatially-explicit Habitat Suitability Indices (HSIs) in the form of “predicted occurrence” models (Guisan and Zimmermann, 2000: 169), which often fall at the nexus of empirical, mechanistic, and analytical modeling strategies. They rely on ecologically-significant variables to predict the spatial distribution of a species, often sacrificing precision for generality. Though some cougar habitat models are based on probabilistic metrics derived from measured presence-absence data (i.e. Thatcher et al., 2006), many, including most of those presented here, rely on indirect measures and ecological analogy to identify locations where the species may live. The product of an HSI model is a relative index of habitat suitability reaching across the landscape under study, restricted by the local-level geographic extent of the measurement unit (i.e. pixel size).

While models for *P. concolor* populations and habitat have taken many forms over the years, the majority of studies are focused on Western source populations. Outside of Florida and its immediate vicinity, modeling for cougars in the East is limited. Of the spatially-explicit habitat models focused on the East and near Midwest, they follow similar conceptual approaches (see Appendix A for an Overview of Modeling Approaches and a Summary of Replicated Model Structures). Taverna et al. (1999), Moye (2007), and Anco (2011) each present HSI models with relatively straightforward structures. Taverna et al. (1999) offer a model for the Central

Appalachian Mountains. Relative to other HSIs, unique features include a measure of prey density, and relatively coarse-grained analysis. Moye (2007) presents an HSI model for the Southern Cumberland Plateau that uses, among other predictors, two measures of landscape fragmentation. Her model does not include data on either human population density or prey abundance. Anco (2011) presents a basic univariate model based on forested land cover, but does not include predictor variables that generally hold across different bioregions (e.g. anthropogenic disturbance).

LaRue and Nielsen (2011, originally in LaRue, 2007) and Thatcher et al. (2003, 2006) present models with more complex structures than those noted above. The former used Analytic Hierarchy Process (Saaty, 1980) to quantify expert opinions for model parameterization in the Midwest. Their model does not include any measure of prey abundance. Thatcher et al. (2003, 2006) present a multi-pronged analysis for the Southeast based off empirical data from Florida panthers. Their landscape-scale empirical model is applicable to other regions, while their local-scale statistical model, metapopulation model, and expert assisted models are specific to their landscape-scale model results and their study region. The authors felt that given South Florida’s unique ecological conditions (i.e. more feral hogs than deer), some of the important habitat predictors, such as prey density, should not be incorporated into their empirical model.

Laundré (2013) provides the only cougar habitat model for the Northeast specifically – a Population Viability Analysis (PVA) for cougars in New York’s Adirondack Park. The approach is essentially a dual-component analysis looking at prey availability and forested land cover. Because of limited understanding in how cougars might use the Northeastern landscape, the use of complex models that rely on fine-scale habitat predictors was avoided (J. Laundré, SUNY Oswego, personal communication). Instead, Laundré evaluated habitat availability after removing buffered roads, buffered human settlement, and aquatic features from the landscape. In the Adirondack region, this leaves primarily forested land cover.

I sought to expand on previous modeling endeavors to understand (1) where in the Northeast cougars would potentially occur, and (2) whether there is enough habitat in the region to support a viable cougar population. My research addressed these questions by developing a series of spatially-explicit, predictive HSI models for the broader New England region.

2. Methods

2.1. Study area

I evaluated cougar habitat suitability in the six New England states, in addition to that portion of New York that lies East of the Hudson River and its longitudinal projection Northward (Fig. 1) – hereafter referred to as New England or the Northeast. This area represents a diverse bioregion with four distinct seasons and temperature extremes akin to regions further to the North and South (Alden and Cassie, 2005). The Northeast is famous for its acidic, granite-laden soils, and supports a wide-range of forest structures. Boreal forest is common in the Northern reaches, gradating to mixed hardwood and coniferous forests in the South (Kricher and Morrison, 1998). Coastal sites, major river valleys (e.g. the Hudson and Connecticut), and mountain ridges provide additional floristic variation. The elevation ranges from sea level at the coast to 1916 m at the top of Mount Washington, the highest point in region. Average annual precipitation is generally between 80 and 125 cm of rain, and 60 and 300 cm of snow (Alden and Cassie, 2005). The region supports a wide variety of fauna, of which moose (*Alces alces*) are notable in the Northern reaches, and white-tailed deer

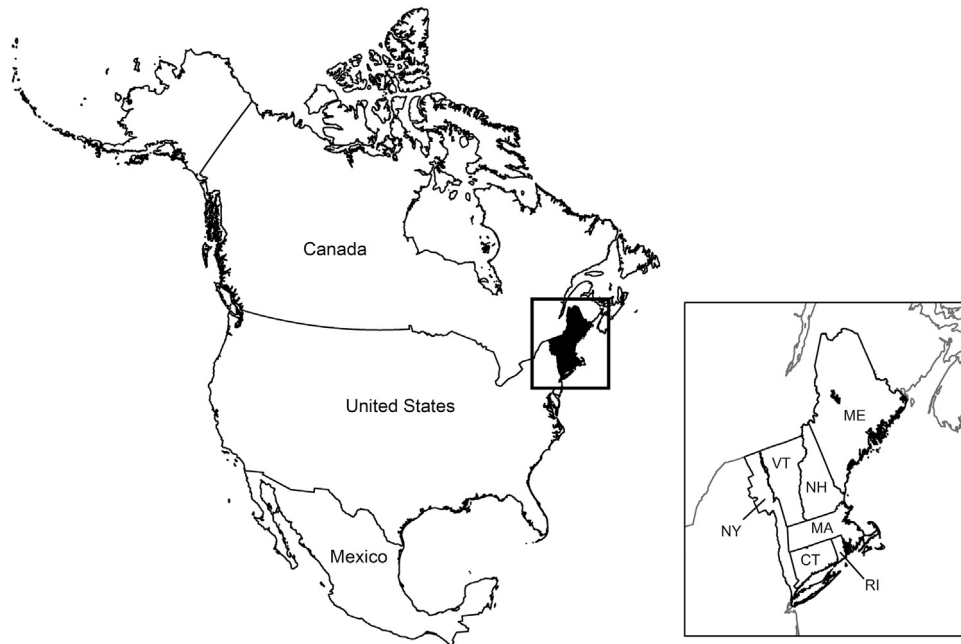


Fig. 1. The study region, including the area subsumed by the six New England states and the portion of New York East of the Hudson River.

(*Odocoileus virginiana*) are abundant in Southern reaches. While the historic Eastern cougar's range encompassed portions of Quebec, New Brunswick, and Nova Scotia that are adjacent to the study site (Young and Goldman, 1946; Culver et al., 2000), I did not examine Canadian habitat due to limitations in data availability.

2.2. Model design

This work was designed to produce a set of heuristic tools that could shed light on where potential cougar habitat might occur within the region. *P. concolor* was extirpated from the Northeast before thorough documentation of its habitat preferences had been established. While using ecological predictors from analogous bioregions (e.g. Thatcher et al., 2006, or LaRue, 2007) makes sense where the geographic proximity between the current population and the predicted site(s) is not extreme, the Northeast lies over 1600 km and nearly 20° of latitude from the nearest known source (*P. concolor coryi* in South Florida). Because of this, questions of the efficacy of using ecological analogy arise. I addressed these challenges by using a Geographic Information System (GIS) to (1) replicate the methods from five spatially-explicit raster-based HSI models developed for other locations; (2) build original GIS HSI models using alternative combinations of relevant predictor variables; (3) perform casual assessments of model agreement by combining individual models into two ensemble models; and (4) evaluate each model by comparing the proportion of forested land cover present at the sites of historic cougar kills to the viable habitat identified by both individual and ensemble models. This approach sought to find a compromise between the strengths and weaknesses of each model, because even common cougar habitat predictors, such as land cover, vary significantly between bioregions (e.g. moist lowlands in Florida versus rugged mid-slope in the West).

2.2.1. Data structure

ArcGIS 10.0/10.1 (ESRI, Redlands, California) and FragStats 4.1 (FragStats v. 4.1, <http://www.umass.edu/landeco/research/fragstats/fragstats.html>, accessed 5.10.12) were used to develop and manipulate geospatial data. A set of core predictor data

layers served as the foundation from which I extracted model-specific datasets. The acquisition of raw data and the development of these model-specific datasets are fully detailed in Appendix A – Details on Data Structure. Briefly however, core datasets included a regional road network, hydrographic features, land cover, a digital elevation model, human population density, and prey density. To the author's knowledge, the two core prey density datasets, established using five years of harvest data for each township in the study area, are the finest scale data of its kind to be applied in a cougar HSI. All datasets were initially built at 30 m resolution and resampled to match the different modeling strategies I explored.

2.3. Replicated models

I replicated the methods used in five cougar habitat suitability models originally applied to areas outside of my study site: Taverna et al. (1999), Moye (2007), Anco (2011), LaRue and Nielsen (2011), and Laundré (2013). These models were selected for several reasons. First, with the exception of Laundré (2013), they are all a form of HSI, where predictors and/or output fell on a continuous scale of suitability. HSIs may be criticized as overly simplistic, but where the Northeast is data deficient and the rigorous evaluation of predictive models against a stable cougar population is not possible, more complex models can lead to misperceptions of predictive strength. In part, HSIs were selected because they make relatively few assumptions about how cougars would use the region's patchwork landscape. Second, while the outputs of these models are not directly comparable, their continuous value distributions allowed me to index them to a like scale for comparison and aggregation (i.e. ensemble models). Third, as exploratory research, I hoped to capture a range of variability in predicted habitat that is not visible when a single model is employed. These models come from varied geographic contexts in and around the historic Eastern cougar's range, and so represent varied perspectives on how cougars are thought to respond to their local surroundings.

Each author relied on numerous sources of information to establish predictors and to parameterize his or her model, including external expert opinions, the author's own opinions, first-hand data, primary and secondary literature. Fundamental model

Table 1
Replicated and original methods used to model cougar habitat in the Northeastern United States.

Authors	Date	Location ^a	Cells (m)	Help ^b	Approach ^c	Variables ^c	Attributes ^d
Taverna et al.	1999	WV, PA, OH, KY, VA	3768.289	N	Variables indexed and summed; equal weight	Human population density, mean by county Deer harvest density (5-year mean by county) Road density (MW km/km ²) Ranked land cover	N N N Y (6)
Moye	2007	TN, AL	90	N	Variables indexed and summed; equal weight	Hardwood forest patch density Contagion Ranked land cover Road density (MW km/km ²)	N N Y (6) N
Anco	2011	GA	30	Y	Binary with MW mean	Binary land cover	Y (2)
LaRue and Nielsen	2011	ND, SD, NB, KS, OK, AR, MI, IA, MN	90	Y	Weighted sum ^e	Ranked land cover Human population density Distance from paved roads Slope Distance to streams	Y (8) Y (4) Y (3) Y (3) Y (3)
Laundré	2013	NY	30	Y	Binary with MW mean ^f	Binary land cover	Y (2)
Glick	NA	ME, NH, VT, RI, MA, CT, NY	30	NA	Variables truncated, indexed and summed; equal weight	MW mean of population density MW mean of 5-year mean male deer harvest by town, normalized by forested cover MW mean of distance to perennial and intermittent water MW mean of distance from paved roads MW mean of percent forested land cover Patch density (MW) Contagion (MW)	N N N Y (2) N Y (6)

^a Original locations where model was applied.^b Help details reliance on authors' input for replication. N = input was not required, Y = input was required.^c MW = moving window analysis.^d Attributes are sub-variables (e.g. individual land cover classes, or distance classes). Numbers in parentheses indicate how many attributes there are for a given variable.^e Weighted sum relied on two tiers of weights, attribute weights and variable weights. Weights were derived using Analytic Hierarchy Process.^f Original model did not include moving window analysis – binary raster was the final output.

components are presented in Table 1, and summaries of model construction can be found in Appendix A – Summary of Replicated Model Structures. For accurate replication, I relied on the original texts and, in some cases, direct correspondence with the author(s). Except where noted (see Appendix A), all models were replicated accurately, given uncontrollable region-specific changes (e.g. number of land cover classes), updated data (e.g. 2006 versus 2001 National Land Cover Dataset), and unit conversion (e.g. mi/mi² to km/km²). In the case of Anco (2011) and Laundré (2013), the methods that I mimicked served as portions of larger studies.

2.4. Original model

Across varied bioregions cougars tend to select for similar habitat. Their preferences for areas of low anthropogenic influence, a healthy cervid population, and enough unoccupied territory to support non-overlapping male home ranges and partially overlapping female home ranges (Hornocker and Negri, 2010) suggest that cougar habitat is somewhat consistent and predictable. There is

a growing body of literature however, that suggests that cougars have a high capacity to adapt. A variety of recent findings help to exemplify the ways in which this species' behavior deviates from some traditional assumptions. For example: Nevada, is serving as a source population of dispersing cougars, while California is serving as a sink (Andreasen et al., 2012); a cougar has been living in Los Angeles' Griffith Park (Groves, 2012); a cougar dispersed over 2400 km from South Dakota to Connecticut (Drake, 2011); cougars are crossing Florida's Caloosahatchee River (Maehr et al., 2002); and cougars are crossing major interstates (Thompson, 2009; Drake, 2011). In this light, I expanded on previous efforts by exploring models that minimized the use of discrete thresholds in data values. Because discrete thresholds can limit our perceptions of available habitat and behavioral choices, whenever possible I created continuous prediction surfaces that captured the full range of habitat from better to worse. Habitat next to an interstate or suburban housing tract might not be ideal, but cougars may still use it.

The variables I used to predict cougar habitat can be viewed as a triad. There are (1) those reflecting anthropogenic disturbance,

including human population density by township and distance to paved roadways; (2) those reflecting environmental conditions, including distance to perennial and intermittent water features, forested versus non-forested land cover (where agricultural land was lumped with the non-forested class), and average white-tailed deer density by township; and (3) those tied to landscape structure, including forest patch density and overall contagion. Details on the variable development and the rationale for their selection are presented in Appendix A – Original Model Development.

With variables in hand, I modeled habitat using a two-tiered approach. Data were first processed at a fine resolution (30 m) before smoothing to reduce the effects of influential outlying values. The initial values of each model input were then truncated to meaningful value ranges before linearly indexing them to a 0–1 scale. Truncation thresholds were based on empirical data and expert opinions from studies of the Florida panther and Black Hills cougar populations, which are the most geographically and ecologically similar to the Northeast, respectively. I then subjected the indexed predictor variables that were not derived through moving window functions (i.e. not land cover, patch density, or contagion) to a moving window function to average (i.e. smooth) cells values within a circular area 4886.25 m in radius (75 km²). This area corresponds to the size of the smallest female cougar home range in the Black Hills of South Dakota (Fecske, 2003).

I built many spatial models using derivations from the primary datasets noted above. While a few models did not sufficiently exclude urban development from predicted habitat, most offered very similar portrayals of habitat in the region given multicollinearity between predictor variables (i.e. forested terrain and low human population density are generally well aligned). As heuristic tools, and with no data against which to compare each model, no one result was verifiably better than another. However, the model I have chosen to present was parameterized with specific thresholds derived from long-term field studies in other regions, and is the first model of its type to include such fine resolution data on prey abundance, particularly at a regional scale. In these respects, it represents a refinement over the other models presented, and satisfies the core goal of producing a set of heuristic tools to help biologists learn about cougar habitat potential in the Northeast.

2.5. Model unification

The independent structure of each model (including five replicated and one original) provides a unique lens through which to consider predicted habitat. To provide a way to directly compare and to merge spatial outputs, I sought to unify the disparate models. I followed a conceptual approach used by Thatcher et al. (2003, 2006) and LaRue and Nielsen (2011), in which suitable habitat was identified not solely by a given cell value, but by a function of how each cell fit within the local context of surrounding cells. For each completed model output, which ranged in resolution from 900 m² cells (30 m × 30 m) to 14.2 km² cells (3768.289 m × 3768.289 m), I used a circular moving window 4886.25 m in radius (75 km²) to assign each cell the mean suitability score from an area the size of the smallest female cougar home range in the Black Hills of South Dakota (Fecske, 2003) – the most analogous cougar-occupied ecological system to the Northeast. This served to “smooth” output values, and to provide a more realistic expression of real-world transition from location to location.

After smoothing, I extracted the top 25% of values according to the original range of values identified by the pre-smoothed model output. This subset represents the “most suitable” predicted habitat, where we might expect cougars to take up residence if no other physical or anthropogenic barriers were in place. This threshold

accords with LaRue and Nielsen’s (2011) findings that cougars in the Black Hills, SD utilized the top 25% of relative suitability values based on their particular model. In that I replicated these authors’ model directly (see Appendix A), I chose to extend this threshold across all models to delineate the “most suitable” habitat using a shared approach.

After extracting the top 25% of suitability values, I applied a region grouping function to the top ranking cells. Using both four- and eight-cell connectivity rules, region grouping provided a means of identifying contiguous habitat parcels large enough to support viable breeding populations according to two estimates. Beier (1993) found that corridors connecting viable habitat significantly reduced the requisite land area required to sustain a population of cougars over 100 years (600–1200 km² with corridors versus 1000–2200 km² without corridors). I chose the intersection of Beier’s figures, 1100 km², as the liberal estimate of required habitat contiguity, and Belden and Hagedorn’s (1993) 2590 km² as the conservative estimate. These contiguous patches are referred to as viable habitat, and represent the most suitable cougar habitat that the region has to offer based on my approach.

2.6. Model coincidence and evaluation

The predictive models presented above were not evaluated statistically, since there is no data against which to compare the results. Instead, ensemble models were used to help reduce the probability of falsely identifying suitable habitat. This was approached in two ways. In the first, the landscape-wide model outputs (e.g. the initial outputs from each model) were normalized by linearly indexing them to a like scale before summing them to produce a meta-HSI. I then isolated viable habitat in the manner applied to all individual models (i.e. extracting top 25%, region grouping). This approach visually amplified better habitat by pooling higher index scores, and enabled casual visual comparison between collective model prediction and individual model prediction.

In the second method, those areas identified as viable habitat by each individual model were directly overlaid to isolate viable habitat that was coincident across all models. I then identified patches that were still of sufficient size to support a breeding population. In this ensemble model, the probability of finding viable cougar habitat at sites identified as having viable cougar habitat is increased, since numerous models predicted such.

In addition, I evaluated viable habitat in all models by comparing the percent forested land cover within each viable habitat patch, to the percent forested land cover present in the vicinity of historic cougar kills from within the study area. Forested growth supports cougar hunting modes, white-tailed deer – the dominant prey species in the Northeast (Sabine et al., 2001; Lesage et al., 2002; Rooney and Waller, 2003), and kitten rearing, and has been found to be the most important predictor of cougar habitat among experts (LaRue, 2007). If the relative proportion of current forested land cover met or exceeded thresholds used by historic animals, then it seemed reasonable to assume that current conditions could support some animals, effectively helping to substantiate predicted habitat. Historic cougar kills were identified in the literature and were included if (1) animal remains had been documented, or (2) the reporting author(s) claimed that an animal had actually been shot, but then escaped. I did not review bounty records. Then, the percent forested land cover present at the time and place of each kill was estimated using relevant literature (Appendix B). These values were aggregated to find an average and range of percent forested land cover used by cougars in the region historically, before comparing them to figures from the present.

Table 2
Suitable cougar habitat identified in the Northeastern United States.

Authors	Top 25% of habitat (km ²) ^a		Connectivity = 4 (km ²) ^b		Connectivity = 8 (km ²) ^c		Forest composition	
	Original area ^d	Top 25% after MW mean ^e	≥1100 (km ²) ^f	≥2590 (km ²) ^g	≥1100 (km ²) ^f	≥2590 (km ²) ^g	Deciduous and mixed ^h	All forest types ⁱ
Taverna et al.	82,090	95,126	83,340	77,475	90,397	89,048	58.0%	75.5%
Moye	74,361	93,936	85,832	84,719	85,832	84,719	62.3%	81.8%
Anco	163,098	163,758	160,971	160,971	160,971	160,971	54.1%	73.2%
LaRue and Nielsen	69,253	75,672	71,296	67,790	71,296	67,791	55.3%	78.7%
Laundré	102,279	36,834	26,682	20,457	26,682	20,457	51.1%	77.2%
Glick	77,024	72,197	63,170	59,925	63,170	59,925	63.2%	76.6%
Meta-Model 1 ^j	79,710	74,701	67,428	67,428	67,429	67,429	58.6%	81.0%
Meta-Model 2 ^k	37,944	11,278	8334	0	10,341	3117	59.8%	86.6%
Historic Forest Cover ^l	Mean = 51.6% ^m	Range = 18–90% ^m						

- ^a Square kilometers of habitat ranking in the top 25% of relative suitability scores.
- ^b Square kilometers of habitat captured by 75 km² moving window averages using 4-cell connectivity.
- ^c Square kilometers of habitat captured by 75 km² moving window averages using 8-cell connectivity.
- ^d Square kilometers of habitat ranking in the top 25% of relative suitability values based on original model outputs, irrespective of contiguity.
- ^e Square kilometers of habitat ranking in the top 25% of relative suitable scores after applying 75 km² moving window average, irrespective of contiguity. Values can exceed original area estimates due to cell reassignment during moving window analysis.
- ^f Square kilometers of habitat contained by parcels ≥1100 km² in size – the intersection of Beier's (1993) estimates for population range size.
- ^g Square kilometers of habitat contained by parcels ≥2590 km² in size – Belden and Hagedorn's (1993) estimate for population range size.
- ^h Percent of contiguous, viable habitat parcels in deciduous and mixed forest types. Does not include shrub-scrub cover types.
- ⁱ Percent of contiguous, viable habitat in any forest cover type, including evergreen cover types. Does not scrub-shrub cover types.
- ^j Meta-Model 1 is that in which each individual model output was indexed to a like scale and summed across models.
- ^k Meta-Model 2 is that in which viable habitat was overlaid to expose coincidence. Interpretation for Meta-Model 2 is unique: the first column = total cellular area in the top 25%, or those cells that had 5 or 6 models align at a given location. The second column is the total cellular area where all 6 models aligned (top 16.67%), regardless of connectivity. The third through sixth columns have normal interpretation, but they speak solely to cells where suitable habitat from all models aligned (top 16.67%).
- ^l Percent historic forest cover from locations of reliable and semi-reliable accounts of cougar. See Tables B.1–B.7 in Appendix B.
- ^m Average and range of individual values for each state contained in Table B.7 in Appendix B.

3. Results

All of the individual models (1) identified habitat that might support cougars, and (2) identified habitat parcels large enough to support one or more viable breeding populations of cougars according to the both the liberal and conservative estimates of requisite area (Table 2 and Figs. 2a–4b). Implementation of Laundré's (2013) modeling approach proved to be the most conservative of the six presented, while implementation of Anco's (2011) approach proved to be the most liberal. In the most conservative of scenarios, being a four-cell connectivity rule paired with Belden and Hagedorn's (1993) estimated minimum population range size of 2590 km², the minimum viable habitat identified by the individual models was 20,457 km² (Laundré model). This can be contrasted with the most liberal scenario, being an eight-cell connectivity rule paired with Beier's (1993) 1100 km², in which the maximum viable habitat identified was 160,971 km² (Anco model). For the first ensemble model, in which each individual model output was re-indexed and added to the others, viable contiguous habitat totaled roughly 67,429 km² in all scenarios. The more conservative ensemble model that isolated coincident viable habitat across all six models, identified between 0 km² of viable habitat in the most conservative scenario and 10,341 km² in the most liberal scenario. That the low end of this range is 0 km² does not mean that no suitable habitat was identified, only that no suitable habitat (i.e. ranking in the top 25%) in contiguous patches large enough to support a breeding population was identified. Disregarding contiguity, when looking across individual models there was between 36,834 km² and 163,758 km² of habitat in the top 25% of suitability values. The mean habitat predicted across all individual models in all scenarios was 80,995 km². The relative standard deviation of individual model predictions was 52.2%, or 49.7% when including the first ensemble model.

Suitable habitat parcels in each model were compared with habitat utilized by historic cougars in New England (Table 2, see also Tables B.1–B.7 in Appendix B). As noted above, forested land

cover is important for cougar hunting and rearing of young, and provides a proxy for deer presence in the Northeast. Where predicted habitat contained as much or more forested habitat as was used historically, additional corroboration is offered in support of predicted habitat. The absence of agreement would not negate habitat suitability, though there would be no region-specific data to support model predictions. Historic percent forested land cover ranged from 18% to 90%, and it is likely that cougars utilized both forested and pasture-based cover that was common to the region at the time (Foster et al., 1998, 2005). The average percent forested land cover in viable habitat patches identified in all individual models and both ensemble models was greater than the mean associated with historic animals (see Appendix B for details). This was the case whether considering deciduous and mixed forest types as a group, or deciduous, mixed, and evergreen forest types as a group.

According to the models presented here, the most suitable cougar habitat within the study site occurs in four largely inter-related regions. The first is in and around the White Mountain National Forest (NH), which is generally rugged, undeveloped mountainous terrain with a mixture of Northern hardwood and mixed hardwood-coniferous forest in the lowlands, and boreal and alpine ecosystems at higher elevations. The second major area of suitable habitat is in and around Baxter Park (ME) and the woodlands to the Park's North and West – a thinly populated region dominated by boreal or mixed boreal-Northern hardwood forest structures. The third site of viable cougar habitat is, at a minimum, the Eastern edge of the Adirondack Park (NY) that was picked up by the spatial extent of these models. The Adirondacks are comprised of rugged, undeveloped terrain dominated by mixed Northern hardwood and boreal forest types, and have already been shown to be suitable cougar habitat (Laundré, 2013). Additional locations that bear strong promise of viable habitat include in and around the Green (VT) and Berkshire Mountains (MA), and in Northern New Hampshire and adjacent portions of Maine. The former are generally rolling hills with mixed deciduous-coniferous forests and unexposed peaks that are less well developed than the surrounding

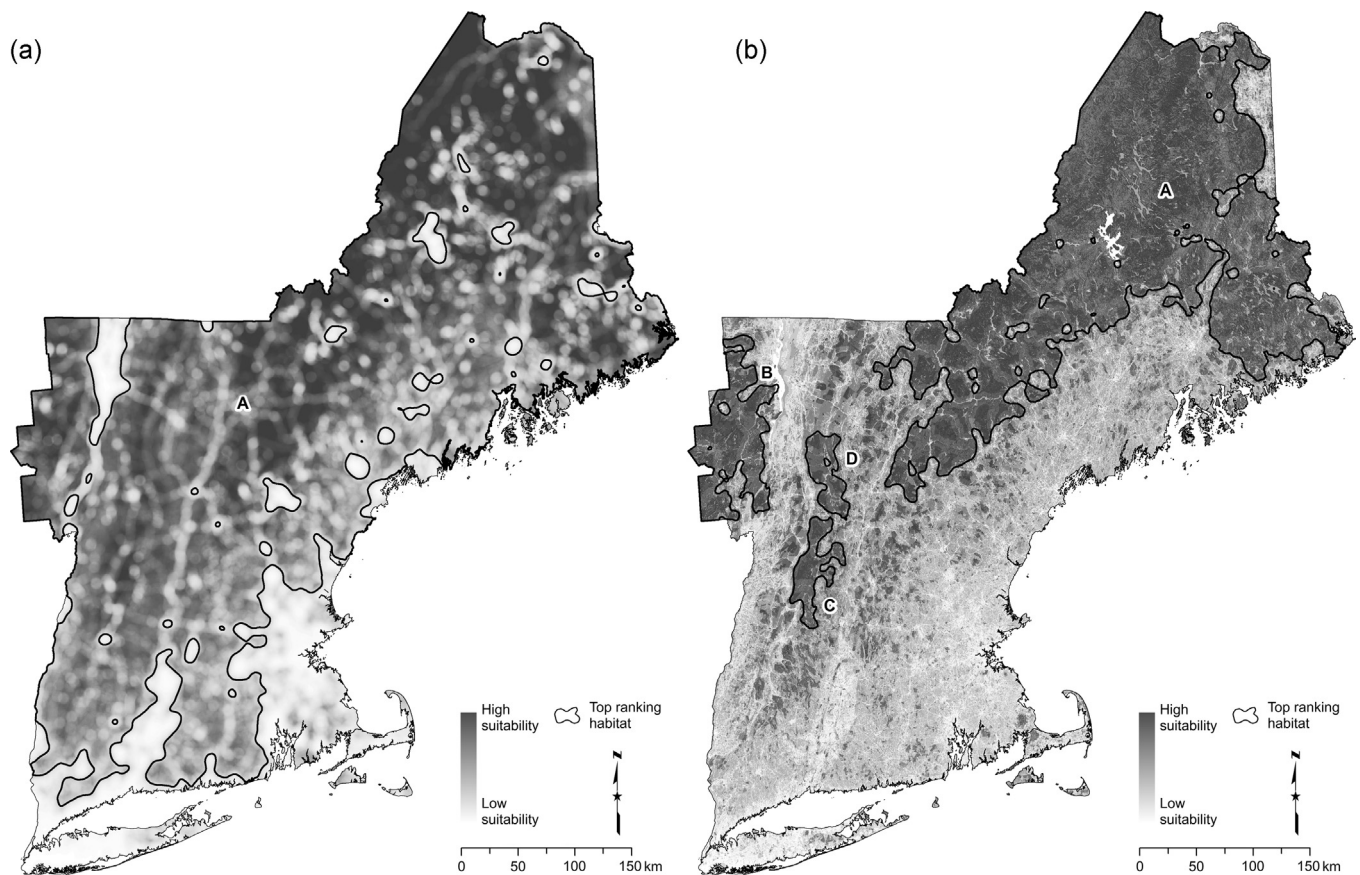


Fig. 2. (a) (Left) Cougar habitat suitability as portrayed through Anco's (2011) methods. Top ranking habitat includes contiguous 30 m cells (8-cell rule) in the top 25% of indexed suitability values, where the single patch is large enough to support a breeding cougar population according to both Beier (1993) and Belden and Hagedorn (1993). A = 160,971 km². (b) (Right) Cougar habitat suitability as portrayed through LaRue and Nielsen's (2011) methods (originally in LaRue, 2007). Top ranking habitat includes contiguous 90 m cells (8-cell rule) in the top 25% of indexed suitability values, where each patch is large enough to support a breeding cougar population according to either Beier (1993, A–D) or Belden and Hagedorn (1993, A and B). A = 61,610 km²; B = 6181 km²; C = 1873 km²; D = 1632 km².

lowlands, while the latter is topographically varied with mixed deciduous and boreal forest types.

While my habitat delineation is in no way a substitute for a proper PVA (i.e. Laundré, 2013), it is still useful to understand the quantity of individual animals that might be supported by the region if predicted viable habitat performed as projected. According to 17 independent estimates generated through capture–recapture studies (Quigley and Hornocker, 2010), cougar densities average 1.57 animals per 100 km² for adults only, and 2.62 cougars per 100 km² for all age classes (my calculations). Using adult densities, which average only 60.1% of all age classes combined, the viable habitat identified by individual models is theoretically capable of supporting between 322 and 2535 cougars, based on Belden and Hagedorn's (1993) and Beier's (1993) population range requirements, respectively. Viable habitat identified by the first ensemble model is theoretically capable of supporting 1062 adult cougars according to both estimates of range requirements. Allowing for eight-cell connectivity, the second, more conservative ensemble model identified viable habitat capable of supporting between 49 and 131 cougars, based on Belden and Hagedorn's and Beier's estimates, respectively.

4. Discussion

With the exceptions of areas in Connecticut and coastal Maine, much of the predicted cougar habitat has relatively low anthropogenic influence, and varied topographic relief. A large percentage of it is associated with the Northern end of the Appalachian

Mountain chain, which contains several large public landholdings. These include Baxter State Park in Maine, the White Mountain National Forest in New Hampshire, the Green Mountain National Forest in Vermont, and the Adirondack Park in New York. Smaller protected areas were too numerous to quantify, for in addition to state-owned land, the Northeast boasts over 600 land trusts (E. Winter, Land Trust Alliance, personal communication) that each manage numerous protected properties. Much of the habitat identified by these models is too rugged for widespread development. Cougars are often associated with rugged terrain in the Western U.S. (Hornocker and Negri, 2010), but it is possible that these areas provide suitable habitat more because of low anthropogenic influence, than because of preferential selection. This is implied by cougar presence in Florida (e.g. Maehr, 1997) among other places. While LaRue and Nielsen's (2011) model is the only one that included slope as a predictor, selecting for steeper areas over flatter areas, all models identified some viable habitat in steeper terrain – likely due to the relationship between terrain and the physical limitations of human development. When slope was tested as a predictor during the development of an original model, I did not find the geographic placement of viable habitat to deviate significantly from models that excluded slope.

The generality of Anco's (2011) and Laundré's (2013) modeling approaches demonstrates the relative utility of simplified habitat prediction. Where cougars once lived in parts of New England that had as little as 18% forest cover (Appendix B), using forest cover as the primary predictor could very well be sufficient for this species. That said, both models identify suitable habitat in close proximity to

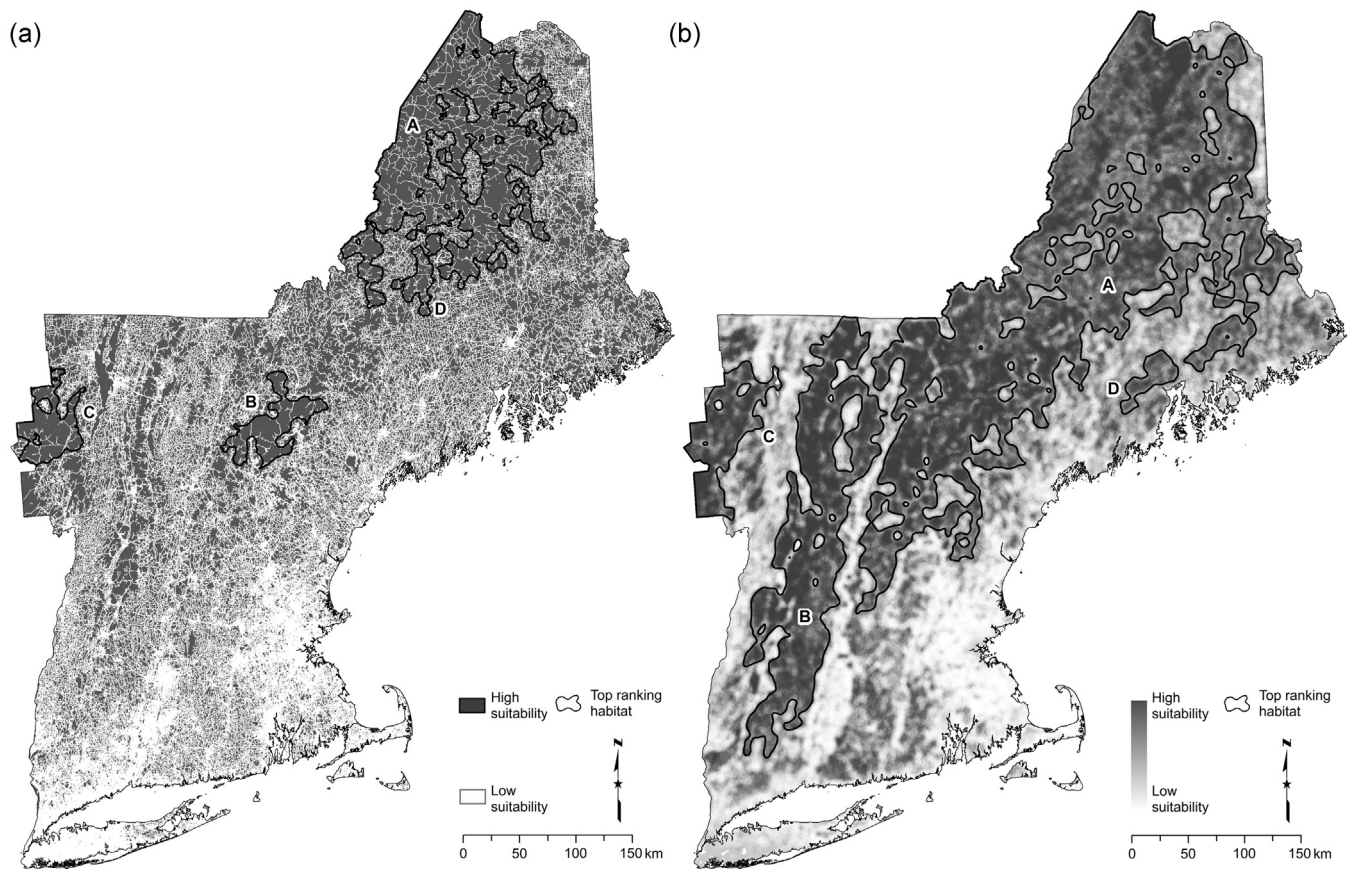


Fig. 3. (a) (Left) Cougar habitat suitability as portrayed through Laundré's (2013) methods. Top ranking habitat includes contiguous 30 m cells (8-cell rule) in the top 25% of indexed suitability values, where each patch is large enough to support a breeding cougar population according to either Beier (1993, A–D) or Belden and Hagedorn (1993 A). A = 20,457 km²; B = 2562 km²; C = 2492 km²; D = 1171 km². (b) (Right). Cougar habitat suitability as portrayed through Moye's (2007) methods. Top ranking habitat includes contiguous 90 m cells (8-cell rule) in the top 25% of indexed suitability values, where each patch is large enough to support a breeding cougar population according to either Beier (1993, A–D) or Belden and Hagedorn (1993, A–C). A = 62,069 km²; B = 17,863 km²; C = 4787 km²; D = 1113 km².

developed regions, such as the Connecticut River Valley. While forest cover does exist in these areas, its relative interspersed, which is only considered in Moye's (2007) model and my own model, might prohibit viable long-term presence. Taverna et al.'s (1999) modeling approach allows for more suitable habitat in the South compared to other models. This is due to the inclusion of prey density averaged at the county level. With four equally weighted predictors, the presence of deer in Southern New England holds 25% of the influence, drawing high suitability scores toward the South. My model also includes prey density, but the fact that it is normalized by forested land cover and one of five predictors helps mitigate such influence.

While both individual and ensemble models identified suitable cougar habitat that met size and contiguity requirements for cougar populations, these predictions must be viewed within the context in which they were generated. It is important, for example, to recognize that the use of moving window functions to smooth suitability values comes at the potential cost of misrepresentation of habitat. Though this technique was employed in several of the models I present, on a cell-by-cell basis, suitability values could be misleading. An urban cell in the center of a rural landscape, for instance, could have an artificially inflated suitability score because of the area around it. That said, my intent was to represent cell-by-cell suitability as a function of the local landscape, effectively mimicking how an animal might perceive its landscape. Without the use of moving window functions, habitat in the Northeast becomes extensively fragmented by roadways, yielding no contiguous parcels suitable for such wide-ranging species as the cougar. And

since we know that many species cross roadways, it seems appropriate to employ moving windows functions to adjust suitability values by context.

Additionally, the models presented have not incorporated input from biologists working in the region (i.e. Thatcher et al., 2006 or LaRue, 2007). The results show relatively good agreement between individual models (Fig. 5a and b), but do not seem optimal given decades of personal experience. Habitat in the Northern half of Maine has relatively low cervid density, with moose being more common than deer (L. Kantar, MEDIFW, personal communication). It seems more likely that cougars would select for areas further to the South that have higher deer densities, despite the fact that those areas also have higher human population density. Other biologists entertain this notion (T. French, MADFG; M. McCollough, USFWS, personal communication). With the adaptability of this species becoming more apparent every year, this does not seem unrealistic. Future modeling might apply greater weight to prey density layers, or include additional data. Snow depth, for example, influences ungulate and cougar movement in other parts of the country (Hemker et al., 1984), and would appropriately reduce regional suitability values in far northern New England.

As habitat generalists, the utility of modeling cougar habitat is tenuous. This is particularly so in a region such as the Northeast, where an absence of reliable data makes it impossible to thoroughly evaluate the results. In many cases, validated evidence from the region has been shown to be from transient animals or released captives (The Cougar Network, 2007; Drake, 2011; McCollough,

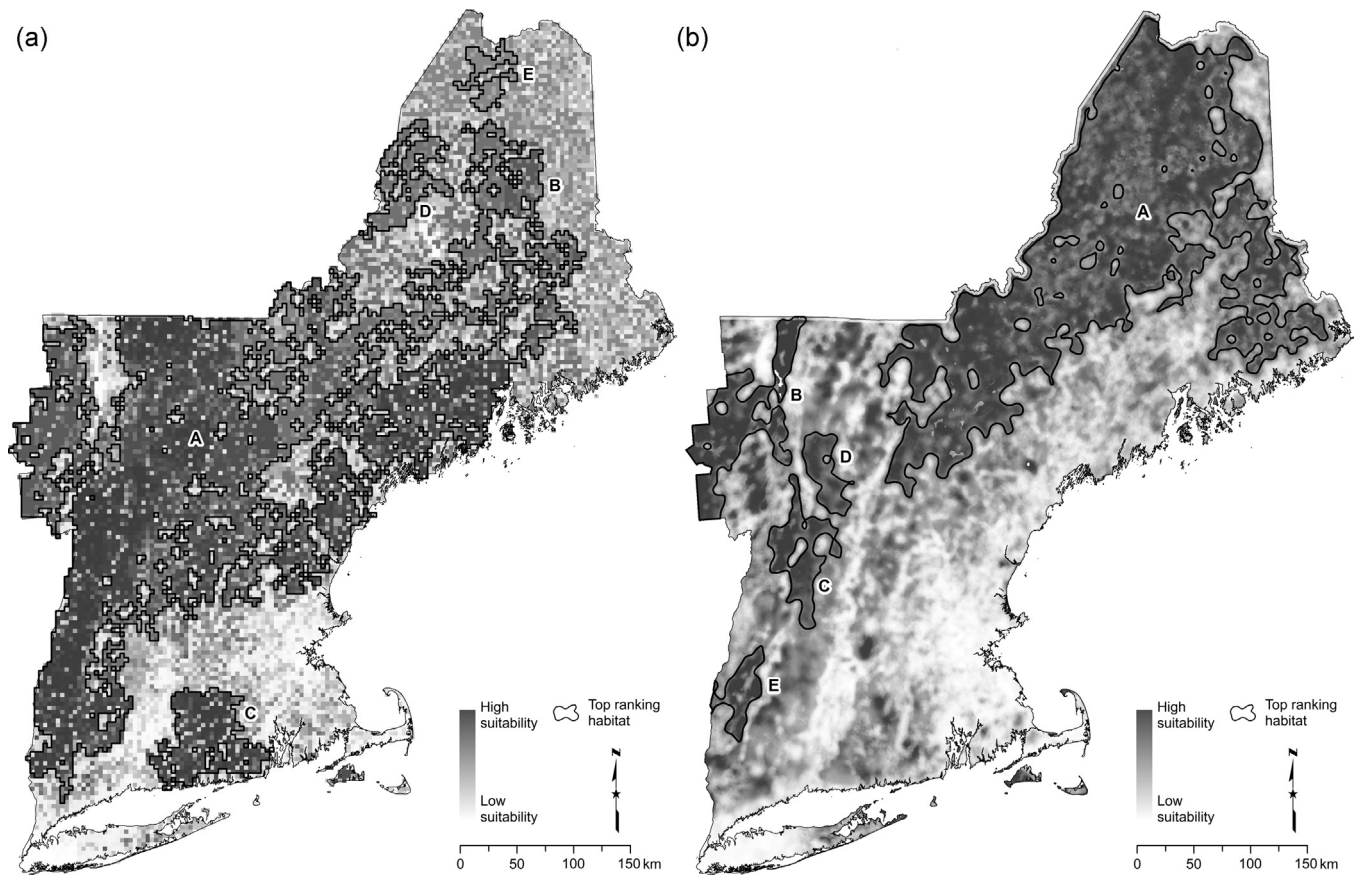


Fig. 4. (a) (Left) Cougar habitat suitability as portrayed through Taverna et al.'s (1999) methods. Top ranking habitat includes contiguous 3768.289 m cells (8-cell rule) in the top 25% of indexed suitability values, where each patch is large enough to support a breeding cougar population according to either Beier (1993, A–E) or Belden and Hagedorn (1993, A–D). A = 76,197 km²; B = 5013 km²; C = 4984 km²; D = 2854 km²; E = 1349 km². (b) (Right) Cougar habitat suitability as portrayed through the author's methods. Top ranking habitat includes contiguous 30 m cells (8-cell rule) in the top 25% of indexed suitability values, where each patch is large enough to support a breeding cougar population according to either Beier (1993, A–E) or Belden and Hagedorn (1993, A–C). A = 51,261 km²; B = 5646 km²; C = 3018 km²; D = 1656 km²; E = 1589 km².

2011), and so does not serve as an accurate representation of cougar behavior. While its use in model validation was not formally considered, between the insufficient quantity of records ($n = 11$) and their spatial distribution, it is unlikely they would be of much use. This dearth of reliable data necessitates ecological analogy as a primary means of informing model development, but since the Northeast lies so far from source populations, analogy may be subject to criticism as well. My choice to use field-derived predictors and parameters from the closest source population in my own model, is a product of wanting to utilize ecologically relevant information. Additionally, I both replicated, and extended across all the models, the methods presented by LaRue and Nielsen (2011). Their model was validate using the second closest source population, and so its application to the Northeast can be seen as similarly reliable, less the confounding effects of longitudinal displacement (which may be significant).

My actual evaluation is limited to using ancillary (historic) data and cross-model agreement to reinforce model predictions and reduce the likelihood of falsely identifying suitable habitat. I fully acknowledge that this approach is insufficient in providing a statistically robust assessment of model accuracy. However, historical analogy and redundancy provided the most reliable means of understanding potential use of the landscape by cougars. If and when reliable signs of cougar presence emerge, the accuracy of predictive models can be properly quantified and iteratively improved through regional field study. The results presented here must be interpreted with care, but we can at least gain insight into the

relative merits and shortcomings of using an HSI approach in a data deficient region.

My general strategy of integrating numerous habitat models and validating against what data does exist, may represent a viable modeling approach for other species that have received attention but for which data deficiency limits habitat prediction on unoccupied sites. Various studies, such as Paquet et al.'s (1999) evaluation of gray wolf habitat in New York's Adirondack Park, have sought to predict habitat in regions where spatial discontinuity between source populations and the study site(s) challenges the efficacy of ecological analogy. Few, however, have sought to overcome data deficiency and spatial discontinuity by capitalizing on the inherent strengths of multi-model synthesis. This approach should not be confused with traditional meta-analysis, which has been employed in ecology for over two decades (Gates, 2002; Gurevitch et al., 2001). While meta-analyses gain strength through the pooling of results from geographically disparate but contextually related studies, my approach gains strength through the pooling of spatially coherent and contextually related methods. That I was unable to locate additional examples of this strategy in the literature is not surprising. Beyond the concerns associated with traditional meta-analysis, such as reconciliation of varied modeling strategies and spatial scales (Cushman et al., 2013), my approach functionally requires study replication, which can be time consuming. While some may argue that predicting habitat under such unfavorable conditions provides little beyond a trained biologist's intuitive sense of suitable habitat, I argue that it not only provides some degree of

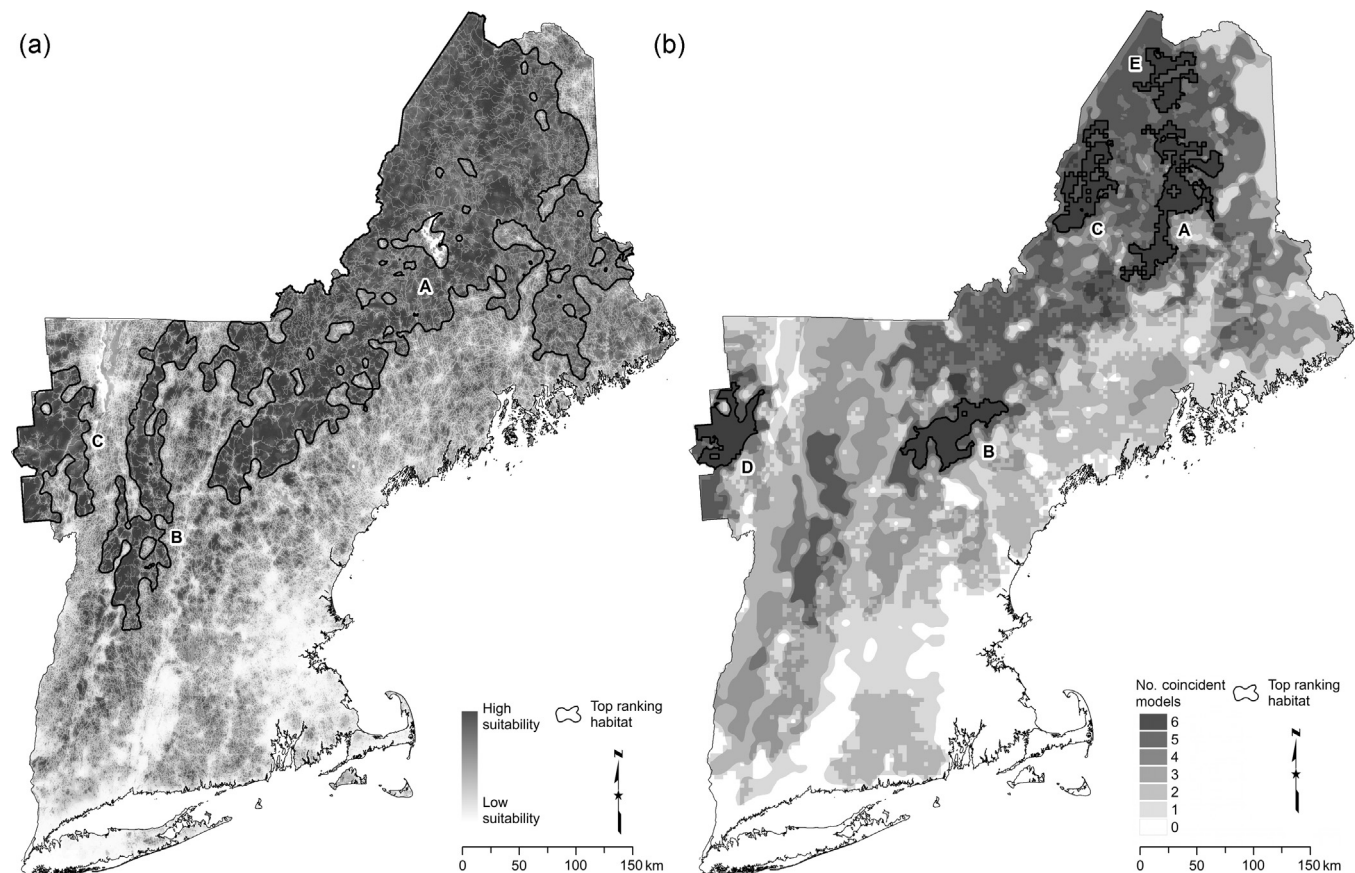


Fig. 5. (a) (Left) Cougar habitat suitability as portrayed through the first meta-model, in which the models presented in Figs. 2a–4b were indexed to a like scale and summed. Top ranking habitat includes contiguous 30 m cells (8-cell rule) in the top 25% of summed suitability values, where each patch is large enough to support a breeding cougar population according to both Beier (1993, A–C) and Belden and Hagedorn (1993, A–C). Coarser resolutions reprojected to 30 m. A = 54,549 km²; B = 7426 km²; C = 5454 km². (b) (Right) Cougar habitat suitability as portrayed through the second meta-model, in which viable habitat patches identified by the models presented in Figs. 2a–4b were directly overlaid to expose coincident habitat (30 m cells). Top ranking habitat includes areas that were identified as top ranking habitat in all six of the individual models (top 16.7% of suitability values), and which were still large enough to support a breeding cougar population according to either Beier (1993, A–E) or Belden and Hagedorn (1993, A). Coarser resolutions reprojected to 30 m. A = 3117 km²; B = 2166 km²; C = 1932 km²; D = 1908 km²; E = 1218 km².

quantitative evaluation, but also allows for spatial visualization, helping to set the course for future model refinement and preliminary management planning.

This research serves only as a preliminary investigation. Future research should focus on: (1) incorporating greater input from regional biologists into model predictions and/or the refinement of model outputs; (2) conducting a proper population viability analysis (i.e. Laundré, 2013), pairing pregnancy, birth, natural mortality, and predation rates for prey with that of cougars to refine estimates of how many cougars viable habitat tracts could support; and (3) examining the relationship between past sighting locations and predicted habitat to assess spatial coincidence and underlying spatial point processes.

4.1. Management implications

As cougars actively expand their current range Eastward (The Cougar Network, 2007; LaRue and Nielsen, 2011; LaRue et al., 2012), it seems only a matter of time until the Northeast is naturally recolonized. My interest was in proactively examining the Northeast's capacity to support an apex predator like the cougar, so that local management agencies could begin to establish guidelines and protocol before the species is present in any appreciable quantity. Given the region's long-term absence of large carnivores, the social carrying capacity for predators that could potentially threaten human well-being or livelihoods, is low. Between regional

eyewitness reports, conversations with locals, and media attention, it is clear that cougars occupy a gray area in the minds of many Northeastern residents. Curiosity and romanticized portrayals of wild New England are common, but fear also plays a prominent role in public perception. While cougar research is not a high priority for management agencies in the region, in part due to resource constraints and in part due to the abundance of unreliable eyewitness accounts, I recommend that public education and preliminary planning be moved off the back-burner as feasible. This will help to alleviate public confusion and hostility that might arise when agencies begin to acknowledge cougar presence and begin active management.

In addition, I recommend that regional management agencies use the models presented here to help shed light on otherwise unverifiable cougar sightings. While many reports are easy to dismiss as cases of misidentification, where this is not the case, sightings can be plotted spatially against the models presented to consider whether or not they fall in viable habitat. This will not add any credibility to a given account, but could help to identify clusters of sightings that beg further inquiry. Since transient dispersers and released captives may not have established home-ranges, this approach can only offer casual support to the field assessments currently performed by biologists.

Finally, I recommend that agencies adopt a unified field record template for tracking cougar sightings, and a companion geospatial database that plots those sightings. If the Northeast follows the

Midwest in increased cougar movement over the coming decades, long-term geospatial documentation of trends from pre- to post-habitation could help to inform studies on “hot spots”, travel corridors, and dispersal trends. Geospatial documentation could also help to shed light on the human social dynamics that serve as prelude to repopulation, and on the unique relationship between pre-habitation sightings and post-habitation sightings.

Acknowledgements

I would like to thank O. Schmitz, G. Longsworth, T. Gregoire, C.D. Tomlin, and L. Bonneau for guidance and technical assistance; and O. Schmitz, P. M. Ashton, E. Hooper, C. Shegrue, J. Clark, E. Raboin, D. Stevens, and my referees for their comments on the manuscript. I would also like to thank M. McCollough and T. French for discussing preliminary modeling strategies, providing access to records, and discussing the fine points surrounding cougars in the Northeast; as well as L. Kantar (MEDIFW), K. Gustafson (NHFGD), A. Murkowski (VTFWD), D. Stainbrook (MADFG), A. Labonte (CTDEEP), H. Kilpatrick (CTDEEP), B. Teft (RIDEM), E. Reed (NYSDEC) and their respective host organizations for providing access to harvest data. M. LaRue, C. Anco, and J. Landré provided useful details on their cougar habitat models. This research was made possible through generous support from the Schiff Fund for Wildlife Research, the Edna Bailey Sussman Fund, the Carpenter-Sperry Fund, and the National Garden Clubs, Inc. Scholarship. These funding sources played no direct role in study design, execution, analysis, or report writing.

Appendices A and B. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.02.005>.

References

- Alden, P., Cassie, B., 2005. *Field Guide to New England*. Alfred A. Knopf, New York, NY, USA.
- Anco, C., (Thesis) 2011. Habitat suitability and reintroduction potential for *Puma concolor* in the state of Georgia. Duke University, Durham, NC, USA.
- Anderson, A.E., 1983. A critical review of literature on Puma (*Felis concolor*). Special Report 54. Colorado Division of Wildlife, Fort Collins, CO, USA.
- Andreasen, A.M., Stewart, K.M., Longland, W.S., Beckman, J.P., Forister, M.L., 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. *Mol. Ecol.* 21, 5689–5701.
- Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.* 7, 94–108.
- Belden, R.C., Hagedorn, B.W., 1993. Feasibility of translocating panthers into Northern Florida. *J. Wildl. Manage.* 57, 388–397.
- Bolgiano, C., 1995. Mountain Lion: An Unnatural History of Pumas and People. Stackpole Books, Harrisburg, PA, USA.
- Bolgiano, C., Lester, T., Donald, L., Maehr, D., 2003. Field evidence of cougars in Eastern North America. In: Harverson, L., Jenks, J., Lindzey, F. (Eds.), *Proceedings of the Sixth Mountain Lion Workshop*. Texas Parks and Wildlife Department Austin, TX, USA, pp. 34–39.
- Clark, D.W., White, S.C., Bowers, A.K., Lucio, L.D., Heidt, G.A., 2002. A survey of recent accounts of the mountain lion (*Puma concolor*) in Arkansas. *Southeast. Nat.* 1, 269–278.
- Culver, M., Johnson, W.E., Pecon-Slaterry, J., O'Brien, S.J., 2000. Genomic ancestry of the American Puma (*Puma concolor*). *J. Hered.* 91, 186–197.
- Cushman, S., Mersmann, T., Moisen, G., McKelvey, K., Vojta, C., 2013. Using habitat models for habitat mapping and monitoring. M. Rowland, Vojta, C. (tech. Eds.), *A Technical Guide for Monitoring Wildlife Habitat*. Gen. Tech. Rep. WO-89. U.S. Dept. of Ag., For. Serv., Washington, DC, USA, pp. 5–1–5–14. <http://www.fs.fed.us/research/publications/gtr/gtr-wo89/gtr-wo89.pdf> (accessed 20.01.14).
- De Vos, A., 1964. Range changes of mammals in the Great Lakes region. *Am. Midl. Nat.* 71, 210–231.
- Dearborn, N., 1927. An old record of the mountain lion in New Hampshire. *Am. Soc. Mammal.* 8, 308–316.
- Doutt, K.J., 1969. Mountain lions in Pennsylvania? *Am. Midl. Nat.* 82, 281–285.
- Downing, R.L., 1982. Eastern Cougar Recovery Plan. U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Clemson, SC, USA.
- Drake, N., 2011. Genes, sightings retrace path of cougar's journey. *Sci. News*, 5–6.

- Fecske, D.M., (Dissertation) 2003. *Distribution and abundance of American martens and cougars in the Black Hills of South Dakota and Wyoming*. South Dakota State University, Brookings, USA.
- Federal Register., 1973. Title 50 – Wildlife and fisheries: chapter 1 – bureau of sport fisheries and wildlife, fish and wildlife services, department of the interior: part 17 – conservation of endangered species and other fish or wildlife: amendments to lists of endangered fish and wildlife. Washington, DC.
- Foster, D., Kittredge, D., Donahue, B., Motzkin, G., Orwig, D., Ellison, A., Hall, B., Colburn, B., D'Amato, A., 2005. *Wildlands and Woodlands: A Vision for the Forests of Massachusetts*. Harvard University, Petersham, MA, USA.
- Foster, D.R., Motzkin, G., Slater, B., 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in Central New England. *Ecosystem* 1, 96–119.
- Gates, S., 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. *J. Anim. Ecol.* 71 (4), 547–557.
- Groves, M., 2012. Mountain lion makes itself at home in Griffith Park. In: Los Angeles Times, 14 August 2012. <http://articles.latimes.com/2012/aug/14/local/la-me-griffith-park-mountain-lion-20120814> (accessed 9.09.12).
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135 (2), 147–186.
- Gurevitch, J., Curtis, P., Jones, M., 2001. Meta-analysis in ecology. *Adv. Ecol. Res.* 32, 199–247.
- Hemker, P., Lindzey, F., Ackerman, B., 1984. Population characteristics and movement patterns of cougars in Southern Utah. *J. Wildl. Manage.* 48 (4), 1275–1284.
- Hornocker, M., Negri, S. (Eds.), 2010. *Cougar: Ecology and Conservation*. The University of Chicago Press, Chicago, IL, USA.
- Kricher, J., Morrison, G., 1998. *A Field Guide to Eastern Forests*. Houghton Mifflin, New York, NY, USA.
- LaRue, M.A., (Thesis) 2007. Predicting potential habitat and dispersal corridors for cougars in midwestern North America. Southern Illinois University, Carbondale, USA.
- LaRue, M.A., Nielsen, C.K., 2011. Modelling potential habitat for cougars in midwestern North America. *Ecol. Model.* 222 (3), 897–900.
- LaRue, M.A., Nielsen, C.K., Dowling, M., Miller, K., Wilson, B., Shaw, H., Anderson Jr., C.R., 2012. Cougar are recolonizing the Midwest: analysis of cougar confirmations during 1990–2008. *J. Wildl. Manage.* 76, 1364–1369.
- Landré, J., 2013. The feasibility of the Northeastern U.S. supporting the return of cougars (*Puma concolor*). *Oryx* 47 (1), 96–104.
- Landré, J., Spatz, C., 2011. Paradise lost: deer, cougars and the decline of the eastern forest. *Wildl. Connection* (Fall), 5–10.
- Lesage, L., Crete, M., Huot, J., Ouellet, J.-P., 2002. Use of forest maps versus field surveys to measure summer habitat selection and sexual segregation in Northern white-tailed deer. *Can. J. Zool.* 80, 717–726.
- Maehr, D.S., 1997. *The Florida Panther: Life and Death of a Vanishing Carnivore*. Island Press, Washington, DC.
- Maehr, D.S., Land, D.B., Bass, O.L., Hootor, T.S., 2002. Florida panther dispersal and conservation. *Biol. Conserv.* 106 (2), 187–197.
- McBride, R.T., McBride, R.M., Cashman, J.L., Maehr, D.S., 1993. Do mountain lions exist in Arkansas? In: Eversole, A., Overacre, K., Jones, E., Konikoff, M., Chapman, B., Brown, J. (Eds.), *Proceedings of the Forty-Seventh Annual Conference of the Southeastern Fish and Wildlife Agencies*. Atlanta, GA, USA, pp. 394–402.
- McCollough, M., 2011. Eastern Puma (=Cougar) (*Puma concolorcougar*) – 5-year Review: Summary and Evaluation. U.S. Fish and Wildlife Service, Maine Field Office, Orono, ME, USA.
- Moye, V.P., (Thesis) 2007. Habitat suitability analysis for mountain lions (*Puma concolor*) on the Southern Cumberland Plateau. University of the South, Seawee, TN, USA.
- Paquet, P.C., Strittholt, J.R., Staus, N.L., 1999. Wolf Reintroduction Feasibility in the Adirondack Park. Conservation Biology Institute, Corvallis, OR, USA.
- Quigley, H., Hornocker, M., 2010. Cougar population dynamics. In: Hornocker, M., Negri, S. (Eds.), *Cougar: Ecology and Conservation*. The University of Chicago Press, Chicago, IL, USA, pp. 59–75.
- Reilly, E.M., 1964. New York's big spooky cat. *New York Conservationist* 18, 2–4.
- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* 181 (1–2), 165–176.
- Saaty, T.L., 1980. *The Analytic Hierarchy Process: Planning, Setting Priorities Resource Allocation*. McGraw-Hill International, New York, NY, USA.
- Sabine, D.L., Forbes, G., Ballard, W.B., Bowman, J., Whitlaw, H., 2001. Use of mixed-wood stands by wintering white-tailed deer in southern New Brunswick. *For. Chron.* 77, 97–103.
- Scott, F.W., 1998. Update of COSEWIC status report on cougar (*Felis concolor cougar*), eastern population. In: Environment Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada.
- Seton, E.T., 1929. *Lives of Game Animals*. Doubleday, New York, NY, USA.
- Spargo, J., 1950. *The Catamount of Vermont*. State of Vermont Free Public Library Commission, Montpelier, VT, USA.
- Stoner, D., 1950. *Extant New York State Specimens of the Adirondack Cougar*. New York State Museum Circular 25, Albany, NY, USA.
- Sunquist, M.E., Sunquist, F., 2002. *Wild cats of the World*. University of Chicago Press, Chicago, IL, USA.
- Taverna, K., Halbert, J.E., Hines, D.M., 1999. Eastern Cougar (*Puma concolor cougar*) Habitat Suitability Analysis for the Central Appalachians.

- Appalachian Restoration Campaign, A Project of Heartwood, Charlottesville, VA, USA.
- Thatcher, C.A., van Manen, F.T., Clark, J.D., 2003. Habitat assessment to identify potential sites for Florida panther reintroduction in the Southeast. Final Report submitted to the U.S. Fish and Wildlife Service, Tennessee, USA.
- Thatcher, C.A., van Manen, F.T., Clark, J.D., 2006. Identifying suitable sites for Florida panther reintroduction. *J. Wildl. Manage.* 70, 752–763.
- The Cougar Network, 2007. Confirmation Map. <http://www.cougarnet.org/northeast.html> (accessed 20.08.12).
- Thompson, D.J., (Dissertation) 2009. Population demographics of cougars in the Black Hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density dependence. South Dakota State University, Brookings, USA.
- U.S.C. (United States Code), 1973. Endangered species act of 16 U.S.C. §1531–1544, Washington, DC.
- USFWS (U.S. Fish and Wildlife Service), 2011. Eastern cougar: questions and answers about the five-year review. <http://nhd.usgs.gov/data.html> (access 10.06.12).
- Wright, B.S., 1948. Survival of the Northeastern panther (*Felis concolor*) in New Brunswick. *J. Mammal.* 29, 235–246.
- Wright, B.S., 1953. Further notes on the panther in the Northeast. *Can. Field Nat.* 67, 12–28.
- Wright, B.S., 1959. *The ghost of North America*, first edition. Vantage Press, New York, NY, USA.
- Young, S.P., Goldman, E.A., 1946. *The Puma: Mysterious American cat*. American Wildlife Institute, Washington, DC.